



## Original Articles

# Projected ocean warming creates a conservation challenge for river herring populations

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The term river herring collectively refers to alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*), two anadromous fishes distributed along the east coast of North America. Historically, river herring spawning migrations supported important fisheries, and their spawning runs continue to be of cultural significance to many coastal communities. Recently, substantial declines in spawning run size prompted a petition to consider river herring for listing under the Endangered Species Act (ESA). The ESA status review process requires an evaluation of a species' response to multiple stressors, including climate change. For anadromous species that utilize a range of habitats throughout their life cycle, the response to a changing global climate is inherently complex and likely varies regionally. River herring occupy marine habitat for most of their lives, and we demonstrate that their relative abundance in the ocean has been increasing in recent years. We project potential effects of ocean warming along the US Atlantic coast on river herring in two seasons (spring and fall), and two future periods (2020–2060 and 2060–2100) by linking species distribution models to projected temperature changes from global climate models. Our analyses indicate that climate change will likely result in reductions in total suitable habitat across the study region, which will alter the marine distribution of river herring. We also project that density will likely decrease for both species in fall, but may increase in spring. Finally, we demonstrate that river herring may have increased sensitivity to climate change under a low abundance scenario. This result could be an important consideration for resource managers when planning for climate change because establishing effective conservation efforts in the near term may improve population resiliency and provide lasting benefits to river herring populations.

**Keywords:** alewife, *Alosa*, bioclimatic envelope, blueback herring, climate change, diadromous, ecological niche, endangered species, fish, habitat suitability.

## Introduction

The effects of global climate change are being realized in natural systems around the world. In general, changes in mean temperature, precipitation, and wind patterns are expected to cause disruptions over the coming decades, and aquatic organisms are already exhibiting a myriad of responses (Walther *et al.*, 2002; IPCC, 2007a; Stock *et al.*, 2011). For instance, ocean warming has been identified as

a driver of distribution shifts observed for many species in the North Atlantic Ocean (Nye *et al.*, 2009; Rijnsdorp *et al.*, 2009; Hare *et al.*, 2010; Lenoir *et al.*, 2011; Pinsky *et al.*, 2013), and climate change will likely continue to alter the thermal habitat of many North Atlantic species (Shackell *et al.*, 2014). Furthermore, environmental variability has been identified as a major source

contributing to changes in fish abundance, and as a factor that can magnify the effects of fishing, which include not only changes in abundance but also changes in population demographics, distributions, trophic interactions, and ecosystem resiliency (Planque *et al.*, 2010; Shelton and Mangel, 2011).

On average, water temperatures have risen in the world's oceans over the past century with continuing increases expected (Levitus *et al.*, 2000; IPCC, 2007b). Temperature is an important feature of aquatic habitat, because it directly influences physiology, behaviour, growth, reproduction, mortality, and therefore population dynamics of marine organisms (Wood and McDonald, 1996; Rijnsdorp *et al.*, 2009). Responses to climate change will vary substantially across species as well as within species according to region, subpopulation, and life stage (Rijnsdorp *et al.*, 2009; Petitgas *et al.*, 2012). Population-level responses to climate change are inherently complex for species with multiple life stages that utilize a range of habitats. Thus, each life stage may be impacted in a unique way because regional dynamics may influence how climate changes will alter individual habitats. In particular, climate change can create bottlenecks in the life cycles of fishes that require a specific spawning habitat (Petitgas *et al.*, 2012). Diadromous species may be particularly sensitive to climate variability and change (Graham and Harrod, 2009) because they require very specific spawning habitat and rely on freshwater (rivers and lakes), estuarine, and oceanic ecosystems. Thus, fully evaluating the effects of climate change on diadromous species requires an integration of ecosystem- and life-stage-specific responses, and consideration of the effects of climate change on system connectivity (Reist *et al.*, 2006).

A comprehensive evaluation of population-level responses of diadromous fishes to climate change is a substantial, data-intensive undertaking that requires synthesis across many disciplines. Yet, effective management of these important natural resources must consider the effects of a changing climate on population dynamics, particularly for species with depleted populations. In response to a petition for listing under the US Endangered Species Act (ESA), the National Marine Fisheries Service conducted a status review of two anadromous fishes: alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*), collectively referred to as "river herring". River herring once supported a substantial commercial harvest that peaked at 74.9 million pounds coastwide in 1958 (ASMFC, 2012). Consequently, populations were depleted over time (Schmidt *et al.*, 2003; Limburg and Waldman, 2009) and recent landings are now only a fraction of the peak. Strict regulations surround directed fishing effort (e.g. five states along the US Atlantic coast have enacted moratoria), but incidental catch of river herring in fisheries targeting Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) remains a concern (ASMFC, 2010; Bethoney *et al.*, 2013a, b). However, caps on river herring bycatch have recently been implemented in the Atlantic mackerel fishery (Federal Register, 2014a) and are proposed for the Atlantic herring fishery (Federal Register, 2014b). Climate change represents a key consideration when projecting long-term population status, and climate effects are now being incorporated into status reviews of fishes (Hare *et al.*, 2012; McClure *et al.*, 2013; Seney *et al.*, 2013). While potential climate effects on river herring were discussed as part of the ESA status review, they were not incorporated into the quantitative models developed for the extinction risk analysis (NMFS, 2013).

River herring are distributed along the North American Atlantic coast from Nova Scotia to Florida (Greene *et al.*, 2009). Blueback herring can be found throughout the geographic range, while

alewife are generally more abundant than blueback herring in the northern portion and do not extend further south than South Carolina. Spawning mostly occurs in spring, but varies with latitude (later in northern rivers) and alewife spawning tends to precede that of blueback herring by a few weeks. River herring are repeat spawners that predominantly utilize natal rivers or lakes for spawning and as a nursery. Human development and dam construction has significantly limited access to historic spawning sites (Saunders *et al.*, 2006; Hall *et al.*, 2011, 2012). However, river herring will establish populations in new systems or re-establish in old systems when conditions become favourable and/or stocking programmes are in place (Loesch, 1987). The freshwater component of river herring has been extensively studied at relatively small spatial and temporal scales (see Greene *et al.*, 2009 for review), but the importance of the marine environment has received less attention. River herring spend most of their lives in the marine realm, arriving as small juveniles, feeding and growing for 3–6 years, then returning to rivers annually for only a short time to spawn (Loesch, 1987). Thus, the effect of temperature on the growth, spatial distribution, and population abundance in the marine realm may strongly influence population dynamics.

In this study, we utilize species distribution models (SDMs) linked to global climate projections to assess the effects of climate change on river herring in their marine phase. A species' distribution and movement can be strongly influenced by the distribution of favourable habitat (Hutchinson, 1957; Holt, 2009). This concept is central to the development of SDMs (also referred to as bioclimatic envelope, ecological niche, and habitat suitability models), which are empirically derived from field-based observations of species and corresponding environmental conditions (Guisan and Zimmerman, 2000; Araújo and Peterson, 2012). Due to their predictive capability, SDMs can be used for projecting the effects of environmental change, and therefore play a prominent role in addressing a range of questions surrounding living resources (Guisan and Thuiller, 2005). Our SDM framework follows a two-component delta (or hurdle) model approach that considers the binomial occurrence of a species as well as total biomass per sample. This allows us to project the probability of occurrence of river herring under various climate scenarios, and also to project changes in relative abundance and density. Many previous studies have examined the probability of occurrence only (Guisan and Zimmerman, 2000; Lenoir *et al.*, 2011; Wenger *et al.*, 2011; Hare *et al.*, 2012; among others), precluding analysis of potential interactions between abundance and environmental change. Further, our study represents the first effort to examine the effect of climate change on river herring.

## Material and methods

### Biological data

We obtained observational data for our study from a fish research bottom trawl survey conducted by the National Marine Fisheries Service's Northeast Fisheries Science Center (Azarovitz, 1981; Sosebee and Cadrin, 2006). The survey began in 1963, but our analyses used data collected in spring research cruises from 1976 to 2012, and fall cruises from 1975 to 2011, because these periods reflect times of more consistent spatial sampling (Sosebee and Cadrin, 2006). We also excluded samples collected at night (after sunset, before sunrise) because river herring were likely more available to the sampling gear during the day (Supplementary data, Figures SA1 and SA2), and there is evidence that these species

undertake diel vertical migrations (Jessop, 1990). We assembled data from each trawl station within our analysis period, including biomass (kg tow<sup>-1</sup>) of alewife and blueback herring captured, and surface and bottom temperature (BT, °C) at the sampling location. Sea surface temperature (SST) and BT were measured at every trawl station initially with expendable bathythermographs and subsequently with conductivity, temperature, and depth instruments. We analysed tow-specific data, and excluded a small number of records that did not have corresponding SST or BT.

The trawl survey range extends from Cape Hatteras, North Carolina into the Gulf of Maine; thus, the survey footprint is nested within the river herring distribution. This precluded our analyses from capturing dynamics at the northern edge of the distribution or in the southern portion (an issue more relevant to blueback herring). While it is important to understand climate effects at the boundaries of distributions, the survey does cover most of the marine distribution of river herring, and we are confident that we characterized dynamics in US waters.

There is strong evidence of stock structure among river herring (NMFS, 2012a; Cronin-Fine et al., 2013; Palkovacs et al., 2013). The number of stocks and their associated boundaries are linked with freshwater spawning habitats, but distinct stocks may be composed of multiple spawning populations. Presumably, marine distributions represent a mixture of separate river herring stocks. Also, the fall survey likely encounters river herring that are migrating southward to aggregate off Cape Hatteras, North Carolina, where the spring survey catches northward migrants, including spawners migrating to their respective spawning habitats (Neves, 1981; Stone and Jessop, 1992).

### Species distribution model

We constructed SDMs, which are essentially empirical marine habitat models, of alewife and blueback herring in spring and fall. River herring exhibit thermal preferences with upper and lower temperature thresholds (Greene et al., 2009), and there is evidence that SST and BT are increasing in our study region (Ecosystem Assessment Program, 2012). To account for potentially non-linear relationships between biomass and temperature, we used generalized additive models (GAMs), which formulate the linear predictor as a sum of smooth functions of the covariates (Hastie and Tibshirani, 1986, 1990). The response variable in SDMs can be binomial presence/absence data or abundance observations (Guisan and Thuiller, 2005); however, we chose a delta (or hurdle)-model approach, which combines two-component GAMs as follows (Aitchison, 1955; Lo et al., 1992; Maunder and Punt, 2004):

$$\Pr(Y = y) = \begin{cases} w, & y = 0 \\ (1 - w)f(y), & \text{otherwise} \end{cases}$$

where  $w$  represents the probability of a species being absent, and  $f(y)$  models a species' biomass using only records where the species was encountered. The delta-GAM approach was useful, because it allowed us to model biomass, a continuous variable, while accounting for many trawl stations where river herring were not encountered (i.e. excessive zeros). We modelled the probability of occurrence ( $1 - w$ ) using a binomial GAM with a logit link function, and the positive biomass records were modelled with a lognormal GAM (i.e. log-transformed biomass, assuming Gaussian error structure and an identity link function). We evaluated Gamma error structure for modelling positive biomass records, but standard model diagnostics strongly favoured the lognormal distribution. We

also found no strong evidence of heterogeneous variance, or temporal or spatial correlation, supporting our model assumptions of constant variance and independence.

We followed Wood (2006) to guide the technical implementation of our binomial and lognormal GAMs, and we considered three predictor variables. The sampling year was included as a factor to capture effects due to changes in total annual relative abundance, while accounting for variable thermal habitat underlying the trawl survey design. Additionally, we considered *in situ* measurements of SST and BT to serve as habitat variables that affect the spatial distribution within a given year. While other abiotic variables, such as salinity, were considered, we assumed that temperature dynamics represent the most important driver of the distribution of anadromous, pelagic species in a marine ecosystem. Therefore, the general structure of a global model developed for the binomial and lognormal GAMs within each species–season scenario can be represented as follows:

$$\text{Response} \sim \text{Year} + s(\text{SST}) + s(\text{BT})$$

where the smoothing function,  $s$ , was configured as a thin plate regression spline for SST and BT. According to the variance inflation factor, we did not observe a high degree of multicollinearity within our global models. Initially, we considered a suite of temperature variables, including lagged and moving average temperatures, but preliminary analyses indicated that *in situ* measurements best explained the variability observed in river herring catches. By focusing on temperature variables, we assumed that a mechanistic relationship between temperature and river herring dynamics underpinned our models. This assumption is supported by several studies that have identified thermal ranges related to various river herring life stages (Greene et al., 2009 for review). When modelling distributions, GAMs offer strong predictive capability, but are often implemented at relatively small spatial scales because they rely on fine scale data. However, we were fortunate to have high-resolution data across a large spatial scale.

We fit a series of binomial (occurrence) and lognormal (biomass) GAMs configured according to the global model structure and all possible nested combinations within each species–season scenario (Table 1). We based our final model selection on Akaike's Information Criterion (Burnham and Anderson, 2002), but also considered the per cent of total deviance explained.

### Climate change projections

Historical climatology in spring (March–April) and fall (September–October) was generated from 33 years (1977–2009) of SST and BT observations across the study region, and projected SST and BT in spring and fall was estimated for two future periods (2020–2060 and 2060–2100). Development of the historical climatology and climate model projections used in our study was described in detail in Hare et al. (2012). We used individual model and ensemble mean temperature projections based on eight atmosphere-ocean general circulation models (AOGCMs) and three greenhouse gas emission scenarios (low: B1, moderate: A1B, and high: A2) from the Fourth Assessment Report (AR4) of the International Panel on Climate Change (IPCC, 2007b, Table 1 in Hare et al., 2012). Rather than using AOGCM output directly for projected temperatures, we used the difference between present and future temperatures estimated by the climate models ( $\Delta T$ ), and added the  $\Delta T$ s to our historical climatology. This “delta”

**Table 1.** Model selection criteria, including per cent deviance explained (% deviance), Akaike's Information Criterion (AIC), and the difference between AIC and the lowest AIC among comparative models ( $\Delta$ AIC) for occurrence and biomass-based GAMs in all species–season combinations.

Model	Occurrence GAMs			Biomass GAMs		
	% deviance	AIC	$\Delta$ AIC	% deviance	AIC	$\Delta$ AIC
Alewife—spring						
1	8.18	7214.59	0.00 <sup>a</sup>	14.97	9779.68	0.00 <sup>a</sup>
2	6.88	7311.88	97.30	12.05	9860.35	80.67
3	6.32	7352.20	137.61	13.94	9807.45	27.77
4	2.03	7672.41	457.82	9.08	9943.44	163.76
Blueback herring—spring						
1	10.77	5784.01	0.00 <sup>a</sup>	22.90	5561.67	0.00 <sup>a</sup>
2	4.79	6161.08	377.07	20.37	5603.91	42.23
3	8.46	5921.65	137.65	20.61	5601.06	39.39
4	2.83	6274.42	490.41	11.23	5755.09	193.42
Alewife—fall						
1	40.58	2296.52	0.54	26.27	2311.57	0.00 <sup>a</sup>
2	40.51	2295.98	0.00 <sup>a</sup>	22.24	2339.58	28.02
3	18.16	3126.31	830.33	24.04	2326.52	14.95
4	1.71	3730.50	1434.52	14.70	2391.65	80.08
Blueback herring—fall						
1	25.98	1244.90	0.00 <sup>a</sup>	35.40	728.36	0.00 <sup>a</sup>
2	24.35	1269.35	24.45	34.40	728.87	0.51
3	15.17	1412.92	168.03	28.43	739.88	11.52
4	9.67	1489.93	245.03	18.46	759.10	30.73

Models compared included: (i) Response  $\sim$  Year +  $s$ (SST) +  $s$ (BT), (ii) Response  $\sim$  Year +  $s$ (SST), (iii) Response  $\sim$  Year +  $s$ (BT), and (iv) Response  $\sim$  Year.

<sup>a</sup>Model selected.

approach adjusted for potential systematic biases in AOGCM climatology (Stock *et al.*, 2011). To address mismatches in the spatial resolution of our historical climatology (0.25° bins) and the AOGCMs (variable across models, but  $<2^\circ$ ), we averaged  $\Delta T$ s across three spatial regions before adding to the historical climatology. Thus, our temperature projections were at the scale of the historical climatology (0.25°), but were derived from  $\Delta T$ s with a coarser resolution. These larger  $\Delta T$  regions were also used by Hare *et al.* (2012), but they found little variability in  $\Delta T$  across space so delineation of these regions does not substantially affect temperature projections. Also, to obtain individual projections over the two future 40-year periods (2020–2060 and 2060–2100)  $\Delta T$ s reflected the averages in each 40-year period.

### Historical trends and future projections

Initially, we used our SDMs to identify thermal preferences for river herring, and estimate historical trends in annual relative abundance for each species by season. Relative abundance was estimated by multiplying annual probabilities of occurrence by annual relative biomass. Probabilities of occurrence were obtained as the back-transformed means for each year from the occurrence GAMs when all variables in addition to “Year” were set to their marginal means (Maunder and Punt, 2004). Annual relative biomass was calculated from the biomass GAMs using back transformation of the coefficients of the “Year” variable with an infinite series lognormal bias correction (Lo *et al.*, 1992). This approach generated estimates of changes in relative abundance observed over the sampling period while accounting for potential effects of dynamic thermal habitats underlying a fixed sampling design.

In addition to estimating historical changes in relative abundance, we projected potential effects of climate change by linking our SDMs to historical and projected climatologies. Because our SDMs were developed using the delta-GAM approach, we could interpret our results in two ways. First, we extracted the occurrence GAM component and generated maps of probability of occurrence over the historical and future periods. Second, we combined the occurrence and biomass GAMs as previously described to generate historic and future maps of river herring density (kg tow<sup>-1</sup>). A fixed year-effect (i.e. relative abundance) was required for estimating spatial dynamics over historical and future periods. This allowed us to test the sensitivity of projected climate effects to river herring abundance; thus, we selected values from years of low, average, and high relative abundance. The high and low years corresponded to the years closest to  $\pm 1$  SD from the mean of the historical abundance trend. The spatial resolution of our projections was equivalent to that of our historical climatology (0.25°). We confined our projections to within the study region because our climatology was developed specifically for that region. We summarized projected climate effects using aggregate mean per cent changes in probability of occurrence and density across the sampling domain, and within four ecological production units (EPUs) previously defined for this region (Ecosystem Assessment Program, 2012): Gulf of Maine (GOM), Scotian Shelf (SCS), Georges Bank (GBK), and Mid-Atlantic Bight (MAB). All quantitative analyses, including data formatting, development of SDMs, linking with AOGCM output, and projections were executed using the statistical programming language R (R Core Team, 2012).

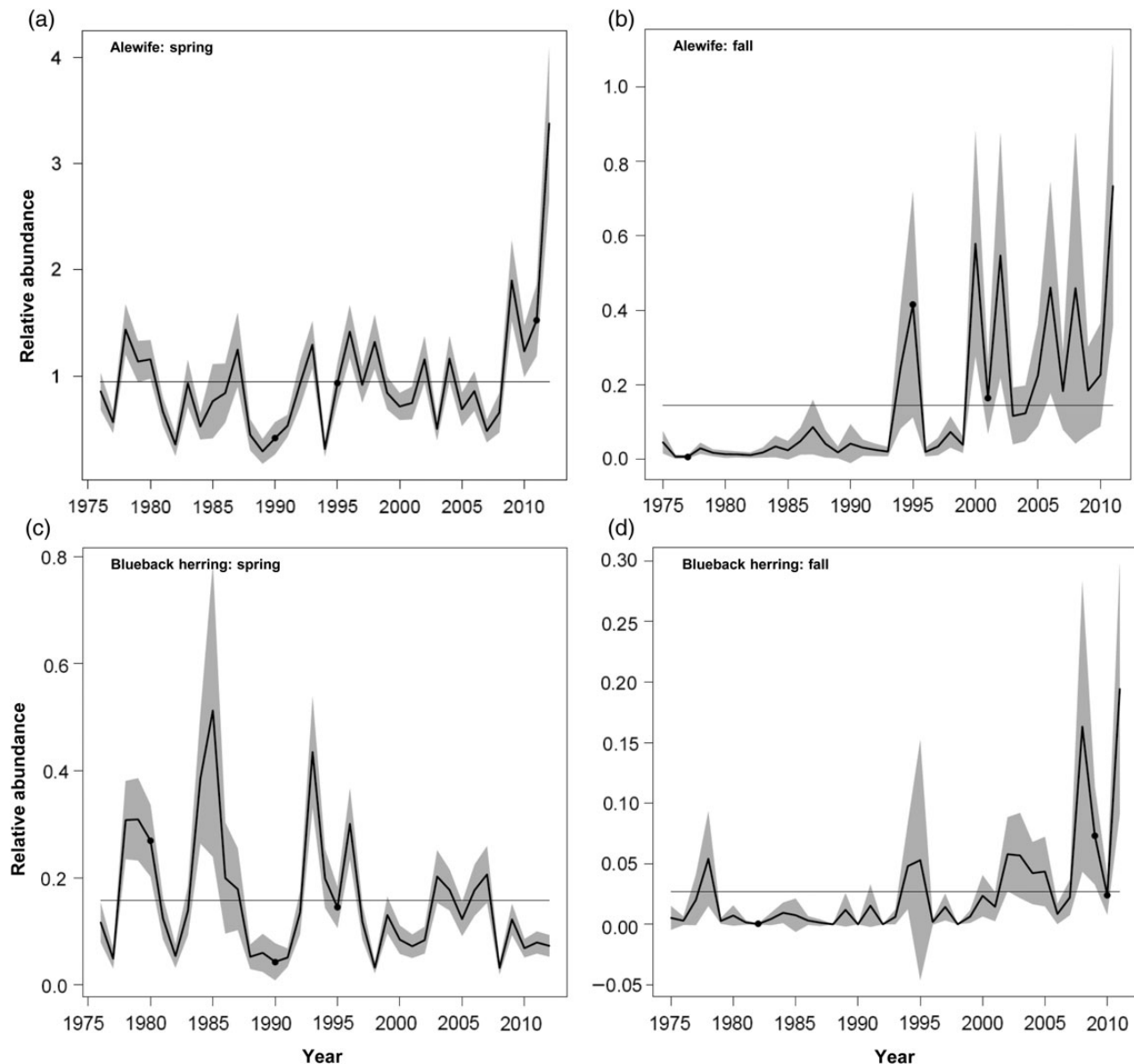
## Results

### Species distribution model

Our seasonal river herring SDMs were developed using 5601 daytime bottom trawl records in spring and 4968 records in fall. The highest encounter rates were observed for alewife in spring (Supplementary data, Figures SA1 and SA2), and on average, river herring sampled in fall were slightly larger in size than those sampled in spring (Supplementary data, Figure SA3). This size discrepancy is not surprising because newly spawned individuals were not likely prevalent in marine habitat during fall (Loesch, 1987), but are encountered by the survey in spring. Over the time-series, negative rates of change in mean size were estimated for all combinations of species and season, with significant size decreases estimated for alewife in spring and fall (Supplementary data, Figure SA3). The declines estimated for blueback herring were not significant in either season.

We used model selection on a series of component GAMs to develop our SDMs. The model with all hypothesized predictors was selected for the occurrence and biomass GAMs for all species–season combinations, except the occurrence of GAM for alewife in fall, which excluded BT as a predictor variable (Table 1). The per cent of total deviance explained by each selected model varied between  $\sim 8$  and 40%. When the per cent explained was relatively low, model diagnostics indicated that this was likely a result of large, homogeneous variance in the data, rather than mischaracterized trends. Our final models suggest that the effects of surface and BT were important factors to include in spring and fall models of alewife and blueback herring. The individual effects of these variables on the response identify SST and BT ranges that exhibit positive or negative effects on density or probability of occurrence





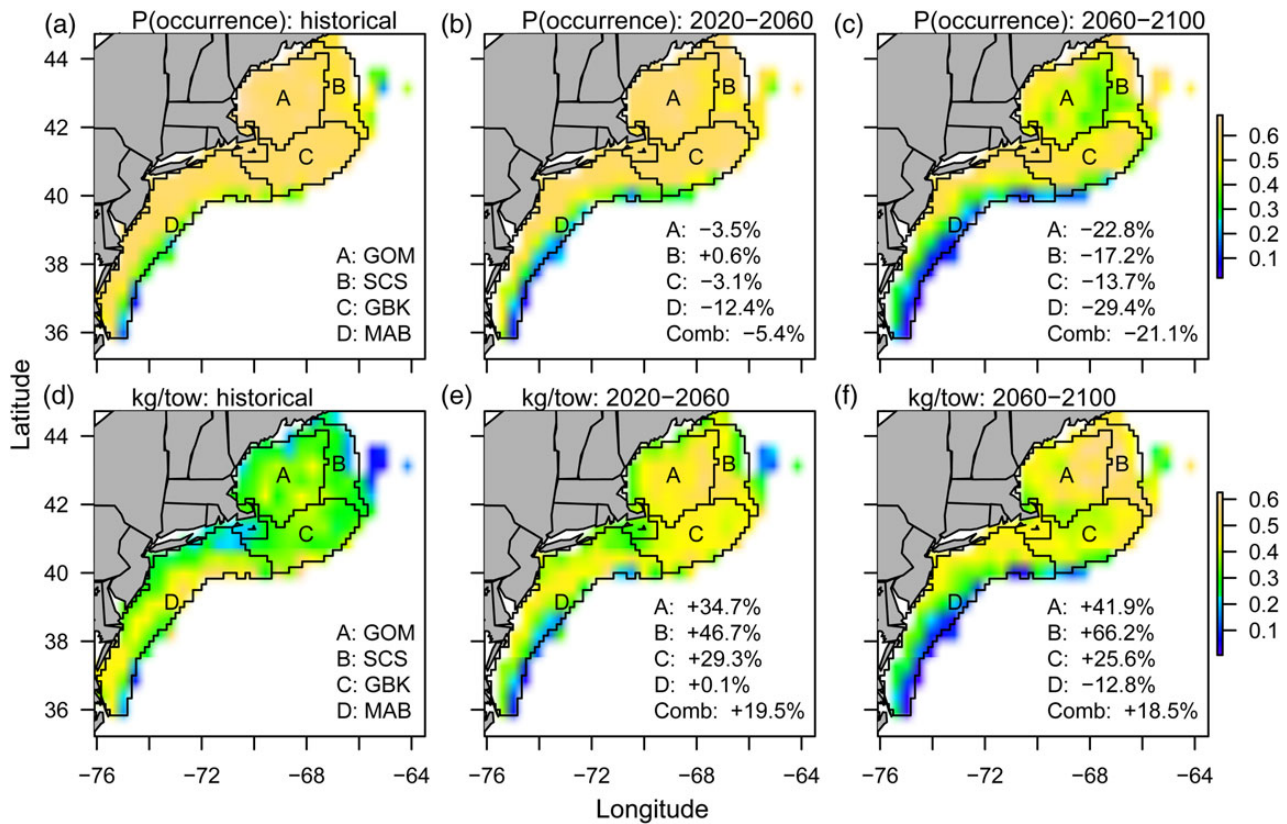
**Figure 1.** Historical changes in annual relative abundance, including mean (black line)  $\pm$  1 standard error (shaded region), estimated by an SDM of alewife and blueback herring in spring and fall in the Northwest Atlantic Ocean. The thin horizontal line reflects mean relative abundance over the time-series.

(Supplementary data, Figures SB1–SB4). In spring, alewife densities were highest over a narrower range of SST ( $5\text{--}8^{\circ}\text{C}$ ) than BT ( $6\text{--}12^{\circ}\text{C}$ ), and probability of occurrence decreased when SST and BT exceeded roughly  $6^{\circ}\text{C}$ . Density of blueback herring increased when SST and BT were greater than  $\sim 6^{\circ}\text{C}$ , whereas probability of occurrence either decreased (BT) or was not affected (SST) above this threshold. In fall, there were negative effects on alewife density and occurrence when SST and BT exceeded  $14\text{--}18^{\circ}\text{C}$ , but the response for blueback herring was less clear (Supplementary data, Figures B1–B4). Variability in temperature effects between occurrence and biomass GAMs provides some justification for following a delta-GAM approach, and may suggest that, in certain habitats, river herring aggregate at higher densities, but are encountered less frequently.

### Historical trends and future projections

The SDMs suggest that alewife abundance has been increasing in the Northwest Atlantic Ocean in recent years, but the trend for blueback herring over the same period is less clear with a small increase estimated in fall and no clear trajectory in spring (Figure 1). These trends are generally similar to those presented using data from the same survey in the most recent river herring stock assessment (ASMFC, 2012). Thus, correcting for potential biases in the survey due to thermal habitats sampled did not change the direction of the trends, but accounting for temperature effects may have resulted in trends that better reflect true fluctuations in abundance.

Our spatial projections indicate that climate change will likely alter the distribution and density ( $\text{kg tow}^{-1}$ ) of river herring throughout much of the study region (Figures 2–5). These projections



**Figure 2.** Historical and future mean probability ( $P$ ) of occurrence (a–c) and density ( $\text{kg tow}^{-1}$ ; d–f) of alewife in spring in the Northwest Atlantic Ocean estimated by linking an SDM with historical climatology and ensemble mean climate projections based on a moderate (A1B) greenhouse gas emissions scenario. Projections assumed an average abundance scenario, and mean per cent changes were estimated for all regions combined (Comb) and for four EPU: (A) GOM, (B) SCS, (C) GBK, and (D) MAB.

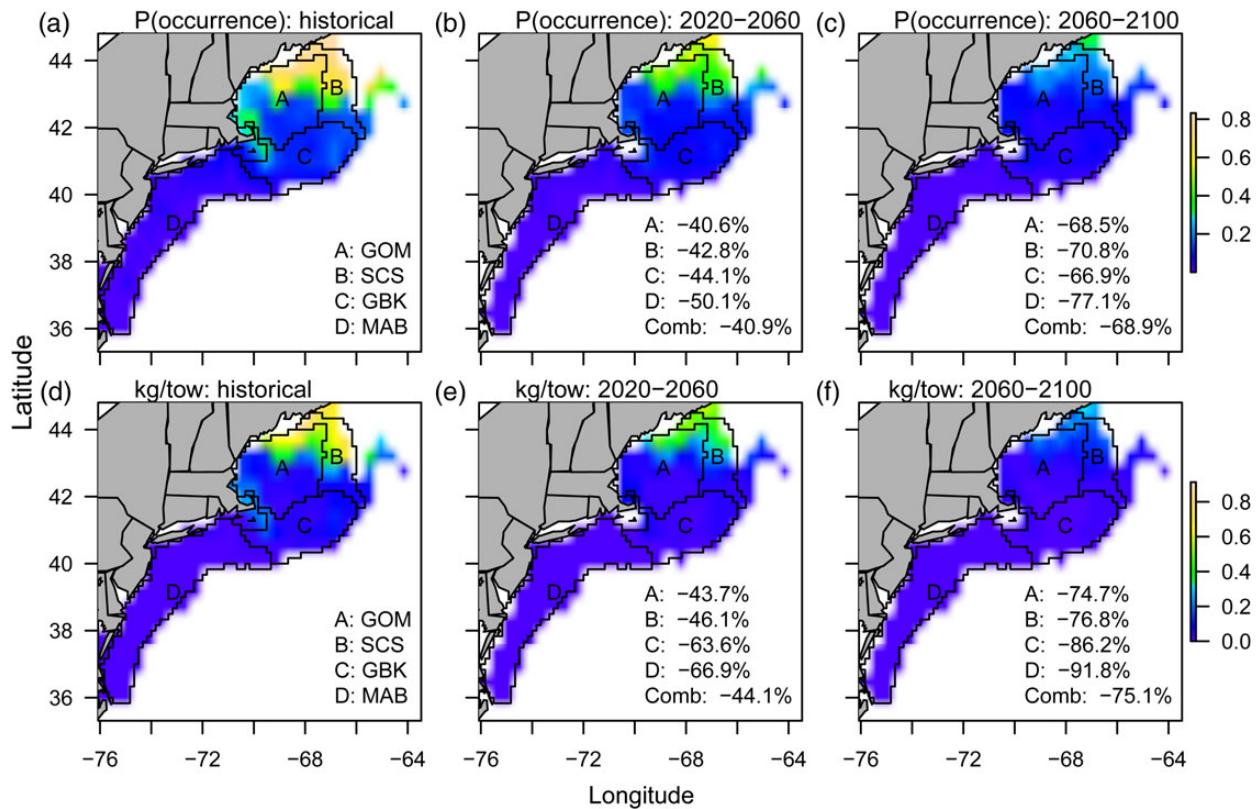
reflect long-term averages rather than exact distributions in a given year, which may vary substantially from the mean. With river herring historically occupying the northern portion of the study region during fall, we projected that ocean warming may cause coast-wide reductions in alewife density, as well as alewife and blueback herring occurrence during this season (Figures 3 and 5). Projections of blueback herring density were more variable with consistent decreases on GBK, but mixed results between projection periods in other regions. Changes in river herring distributions were also projected in spring (Figures 2 and 4). Projections indicated likely decreases in alewife occurrence, particularly in the MAB region, and decreases in blueback herring occurrence in the southern regions, but an increase in more northern regions. With the exception of alewife in the MAB region, projections indicated an increase in river herring density. We focused our spatial projection analyses on the ensemble mean climate projections based on moderate greenhouse gas emissions (scenario A1B) and average relative abundances of river herring, but we also analysed projections based on low and high emissions (scenarios B1 and A2, respectively) and low and high relative abundance scenarios (Supplementary data, Figures SC1–SC8). The general spatial dynamics were consistent across emission scenarios.

To summarize projected climate effects on river herring across the study region, we calculated spatially averaged per cent changes in future probability of occurrence and density (Figures 6 and 7). These summaries accounted for many sources of variability,

including greenhouse gas emission scenarios, individual AOGCM projections, and relative abundances of river herring. Overall, we demonstrated that alewife occurrence will likely decrease continually as ocean temperatures rise, and average density will decrease substantially in fall, but may increase in spring. Similarly, for blueback herring we projected declines in probability of occurrence, a potential decrease in density in fall, and a potential increase in density in spring. However, the projected increase was greater for blueback herring than for alewife, and projected declines were less severe and generally not realized until the 2060–2100 period. The steepest declines were projected for alewife in fall, which may experience up to 80% reductions in probability of occurrence and density. Variability in projections was greater across individual AOGCMs than across emission scenarios (also observed by Hare *et al.*, 2012), and we projected higher sensitivity to climate effects under the low abundance scenario (larger decreases and increases) than for the high or average scenarios (Figures 6 and 7).

## Discussion

By linking SDMs with temperature projections from AOGCMs, we conducted an initial assessment of potential impacts of climate change on river herring. Under the assumption that historical relationships between thermal regimes and river herring distributions will be conserved in the future, we demonstrated that river herring preferred habitat will likely decrease in the Northeast US continental shelf as a result of increasing ocean temperatures. However,



**Figure 3.** Historical and future mean probability ( $P$ ) of occurrence (a–c) and density ( $\text{kg tow}^{-1}$ ; d–f) of alewife in fall in the Northwest Atlantic Ocean estimated by linking an SDM with historical climatology and ensemble mean climate projections based on a moderate (A1B) greenhouse gas emissions scenario. Projections assumed an average abundance scenario, and mean per cent changes were estimated for all regions combined (Comb) and for four EPU: (A) GOM, (B) SCS, (C) GBK, and (D) MAB.

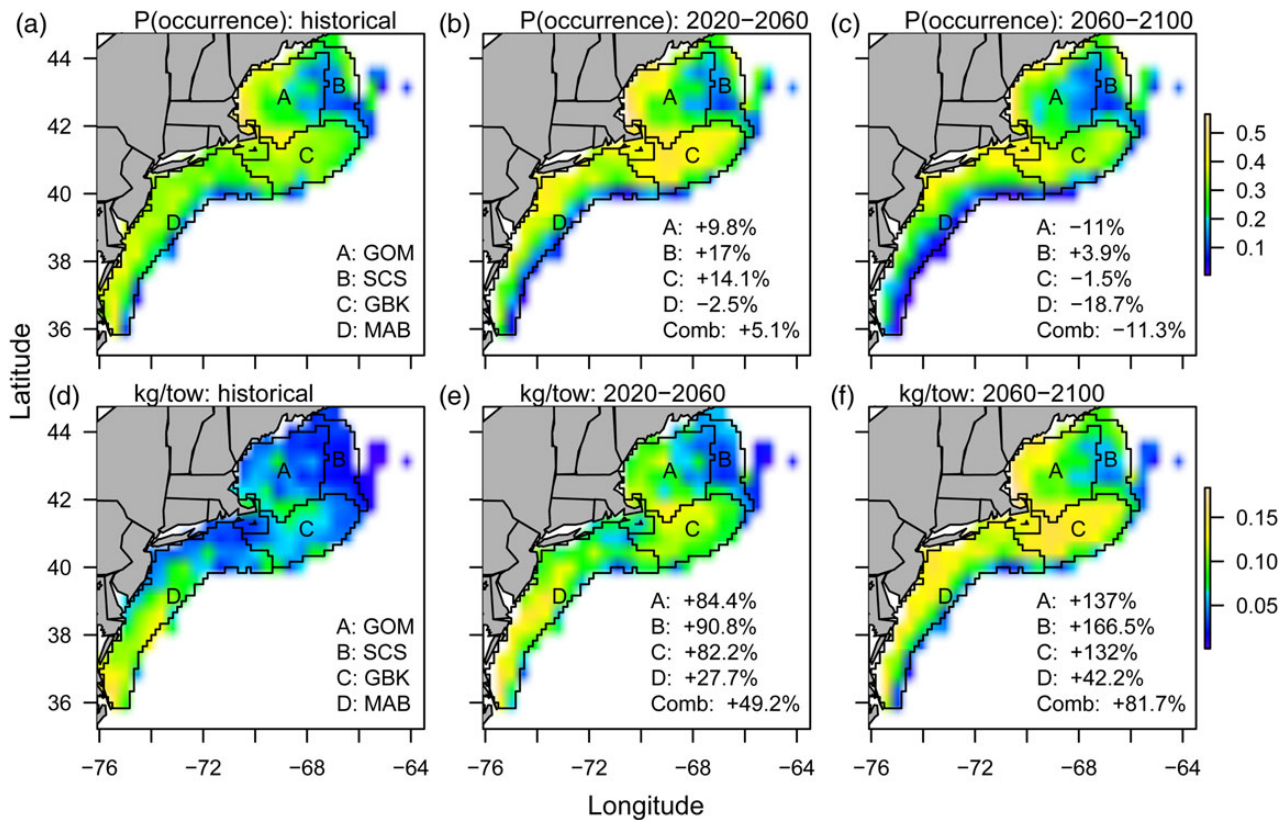
increasing density under certain scenarios (particularly blueback herring in spring) may compensate for losses in other scenarios. Although our models focused exclusively on population and temperature trends in the ocean, river herring dynamics in the marine environment might be considered a species-level response to climate change, integrated across habitats and stocks. The effects of stressors in freshwater habitat on spawning and recruitment success relate to individual spawning runs, but the aggregate effects in freshwater were reflected in the marine trawl survey data. Thus, our assessment of the effects of climate change on river herring was conducted at the metapopulation scale. The SDMs included only climate variables, and therefore did not explicitly consider other important processes, such as biotic interactions. These interactions may influence future river herring populations, but when conducted at large spatial scales, SDMs that include only climate variables are considered suitable for initial projections of climate effects on species distributions (Pearson and Dawson, 2003). Because we evaluated large-scale metapopulations, we are confident that our analyses provide useful initial projections. Nevertheless, future studies that incorporate biotic interactions represent an important methodological advancement that should be pursued.

In addition to assessing climate effects, we used our SDMs to extract historical patterns in relative abundance. The trends estimated in our study are generally similar to those generated for the most recent river herring stock assessment using data from the same bottom trawl survey (ASMFC, 2012), and the small

discrepancies observed can be attributed to differences in modelling approaches. For the stock assessment, abundance trends were estimated using stratified mean number per trawl tow (ASMFC, 2012), where we followed a delta-GAM approach. The trawl survey is based on a randomly stratified design (Azarovitz, 1981; Sosebee and Cadrin, 2006), where survey strata (defined according to depth and area) essentially serve as proxies for habitat. Because survey strata remain fixed over time, systematic changes in the distribution of habitat should be considered when estimating the relative abundance of species like river herring that distribute along habitat gradients and whose range extends beyond the surveyed area. There has been a particularly strong warming signal in the Northwest Atlantic Ocean over recent decades (Belkin, 2009; Shearman and Lentz, 2010), and our SDMs suggest that river herring distribute according to thermal gradients. Thus, by including temperature in our models, we estimated abundance trends for river herring that account for dynamic habitats (i.e. ocean warming) underlying a fixed sampling domain. The GAM approach is frequently used in spatial ecology (Ciannelli et al., 2008), but is less commonly applied when extracting annual abundance trends from fishery-independent surveys because these surveys often follow a randomly stratified design that is thought to account for variable availability to the survey.

Despite increasing trends in river herring abundance in recent years, there is strong evidence that ocean warming will change their distribution and abundance in the study region. The recent increases may have been driven by increases observed in several





**Figure 4.** Historical and future mean probability ( $P$ ) of occurrence (a–c) and density ( $\text{kg tow}^{-1}$ ; d–f) of blueback herring in spring in the Northwest Atlantic Ocean estimated by linking an SDM with historical climatology and ensemble mean climate projections based on a moderate (A1B) greenhouse gas emissions scenario. Projections assumed an average abundance scenario, and mean per cent changes were estimated for all regions combined (Comb) and for four EPU: (A) GOM, (B) SCS, (C) George’s Bank (GBK), and (D) Mid-Atlantic Bight (MAB).

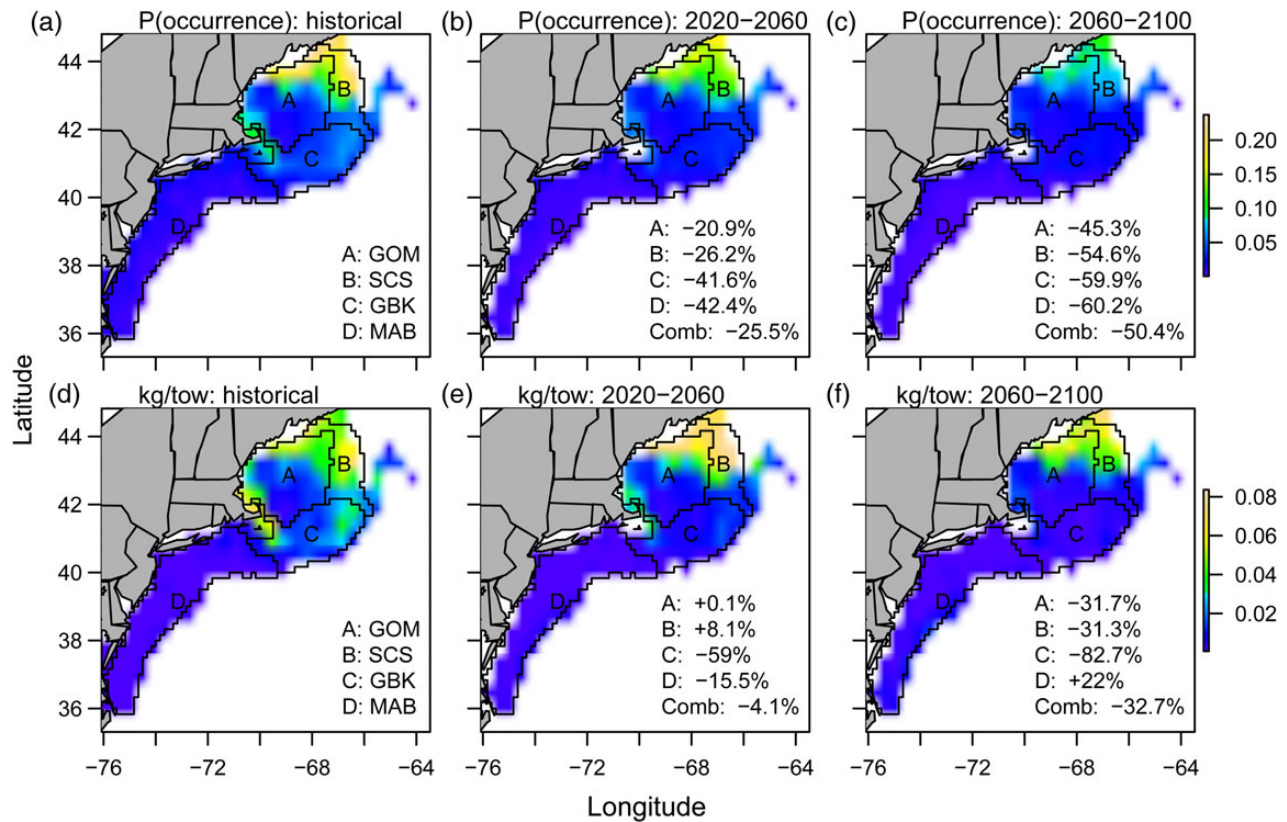
spawning runs in the northern portion of the distribution (ASMFC, 2012). However, assuming ensemble mean projections, we estimate that ocean warming will cause declines in river herring density and occurrence in nearly all combinations of initial abundance (i.e. year-effect), emission scenario, and season by the period 2060–2100. The main exceptions to across-the-board decreases are the increases in density projected in spring, which could serve to buffer the net impacts of climate change on river herring. It may not be surprising that future ocean temperatures in fall are potentially more constraining to river herring than future spring temperatures, because in the study region, water temperature is generally warmer in fall than in spring. Thus, it is more likely that projected ocean temperatures in fall would exceed a thermal tolerance threshold for river herring than in spring. By this logic, increasing summertime water temperatures could represent a key factor influencing oceanic river herring distributions and abundances; however, we did not have river herring or temperature data from summer sufficient to conduct these analyses. It should also be noted that detection rates of river herring were much higher in the spring survey than in fall, so the spring projections were informed by more data. Overall variability in our projections was generally lower in the first period (2020–2060) than in the second (2060–2100), because of a greater divergence in emission scenarios and internal AOGCM dynamics in the later period.

Changing thermal regimes have likely already impacted the distribution of river herring because poleward shifts have been observed over the historical period (Nye *et al.*, 2009; NMFS,

2012b). For many scenarios evaluated, we projected declines in probability of occurrence and density in the southern regions (MAB and GBK), suggesting potential for additional northward shifts. In spring, we projected increases in blueback herring density across regions (especially in the SCS region), and smaller increases in density of alewife (except in the MAB region). Increases in blueback herring density in the southern region (MAB) may actually serve to fill an ecological gap left by declines in alewife density and occurrence. Our seasonal models were entirely independent; therefore, we cannot infer how projected changes in one season will affect the populations in another season. At worst, a universal decline in fall habitat could reflect a bottleneck that negatively impacts future river herring populations, or at best, forces river herring to either adapt to changing conditions or seek suitable habitat outside the study region during fall. This suggests a potentially serious consequence of climate change because in addition to being economically and culturally important species, river herring are important forage fish in coastal ecosystems (Pikitch *et al.*, 2012). With fewer river herring in the study region, the forage base for many important predators in freshwater, estuarine, and marine ecosystems may be reduced coastwide. While declines are likely along the US Atlantic coast, these species may thrive in Canadian waters, and may actually expand into Arctic habitat as temperatures warm (Reist *et al.*, 2006).

Invasion of new regions is one potential mechanism that species can employ to adapt to a changing climate, but it is unclear that this approach will work for river herring. For instance, the degree of



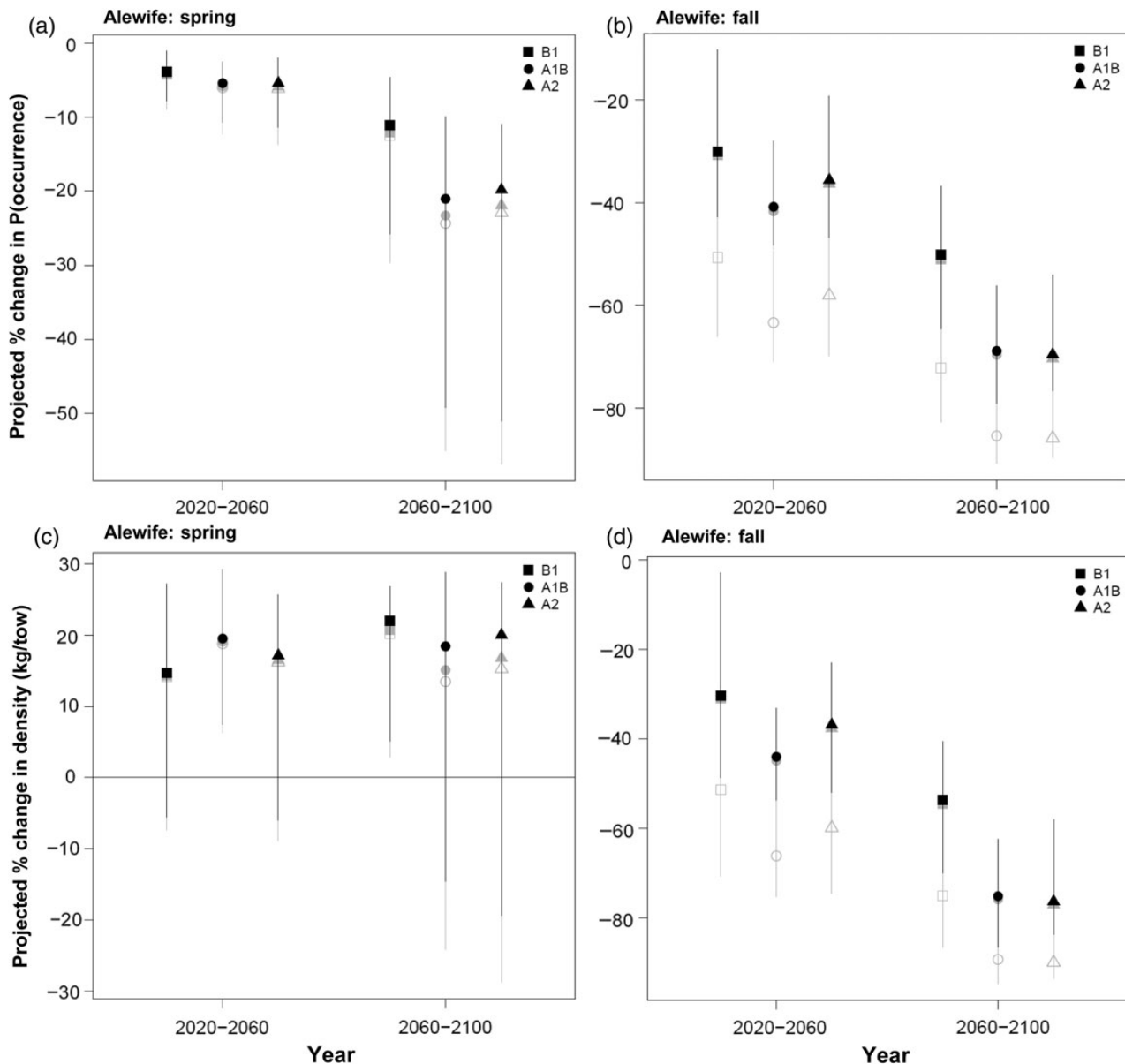


**Figure 5.** Historical and future mean probability ( $P$ ) of occurrence (a–c) and density ( $\text{kg tow}^{-1}$ ; d–f) of blueback herring in fall in the Northwest Atlantic Ocean estimated by linking an SDM with historical climatology and ensemble mean climate projections based on a moderate (A1B) greenhouse gas emissions scenario. Projections assumed an average abundance scenario, and mean per cent changes were estimated for all regions combined (Comb) and for four EPU: (A) GOM, (B) SCS, (C) George’s Bank (GBK), and (D) Mid-Atlantic Bight (MAB).

expansion into polar regions may be limited by the amount of available habitat (Cheung *et al.*, 2009). Also, similar to many anadromous species, river herring show evidence of homing to natal rivers for spawning (Greene *et al.*, 2009). Therefore, if thermal habitats in and/or around river herring spawning locations become unsuitable or marginally suitable, there are four potential spawning responses: (i) selection of new spawning locations; (ii) physiological adaptation to changing thermal habitats; (iii) spawning in unsuitable habitat, which may have negative effects on growth, condition, and mortality; or (iv) avoiding spawning altogether. With responses (i) and (ii), river herring populations may be able to sustain current levels of productivity, where responses (iii) and (iv) represent negative population-level impacts. While Palkovacs *et al.* (2013) observed declines in mean size for river herring collected in freshwater systems, and we detected similar changes over time in marine habitat, these analyses are not able to disentangle climate change from other factors (e.g. density dependence and fishing) that commonly affect growth (i.e. response iii). River herring may be capable of exhibiting response (i) because these species have colonized new systems, but the degree to which straying and homing occur has not been quantified. Homing has been demonstrated in many anadromous species, such as Atlantic (Verspoor *et al.*, 2007) and Pacific salmon (Quinn, 1993) and even in estuarine-dependent species such as weakfish (Thorrold *et al.*, 2001). A high degree of homing could serve as evidence that the species are not adaptable to changing habitats and local extirpation is likely. However,

despite strong homing rates, even a small amount of straying may allow anadromous species to adapt to environmental change. The highly migratory life history of alewife and blueback herring and their ability to osmoregulate under different salinity environments may allow for high plasticity in the response of these species to changing environmental conditions. Yet, this plasticity may also depend on having enough genetic diversity to respond to these challenges. In the United States, stocking of river herring complicates the evaluation of the importance of homing, stock structure, and the adaptive response of river herring to suboptimal temperatures. Using a combination of genetic and demographic analyses, Palkovacs *et al.* (2013) demonstrated that spawning populations in individual rivers can be distinguished genetically, but the multiple riverine populations combine to form fewer distinct stocks (three for alewife and four for blueback herring) along the US Atlantic coast. Thus, there is evidence that river herring stray from their natal rivers within certain geographic areas, but typically not throughout their entire range. We did not feel it was appropriate to project invasions or extrapolate beyond the survey footprint, but given the distinct stock structure of river herring, climate change is likely to cause negative population-level effects, particularly because southern stocks may have a limited ability to seek suitable spawning habitat.

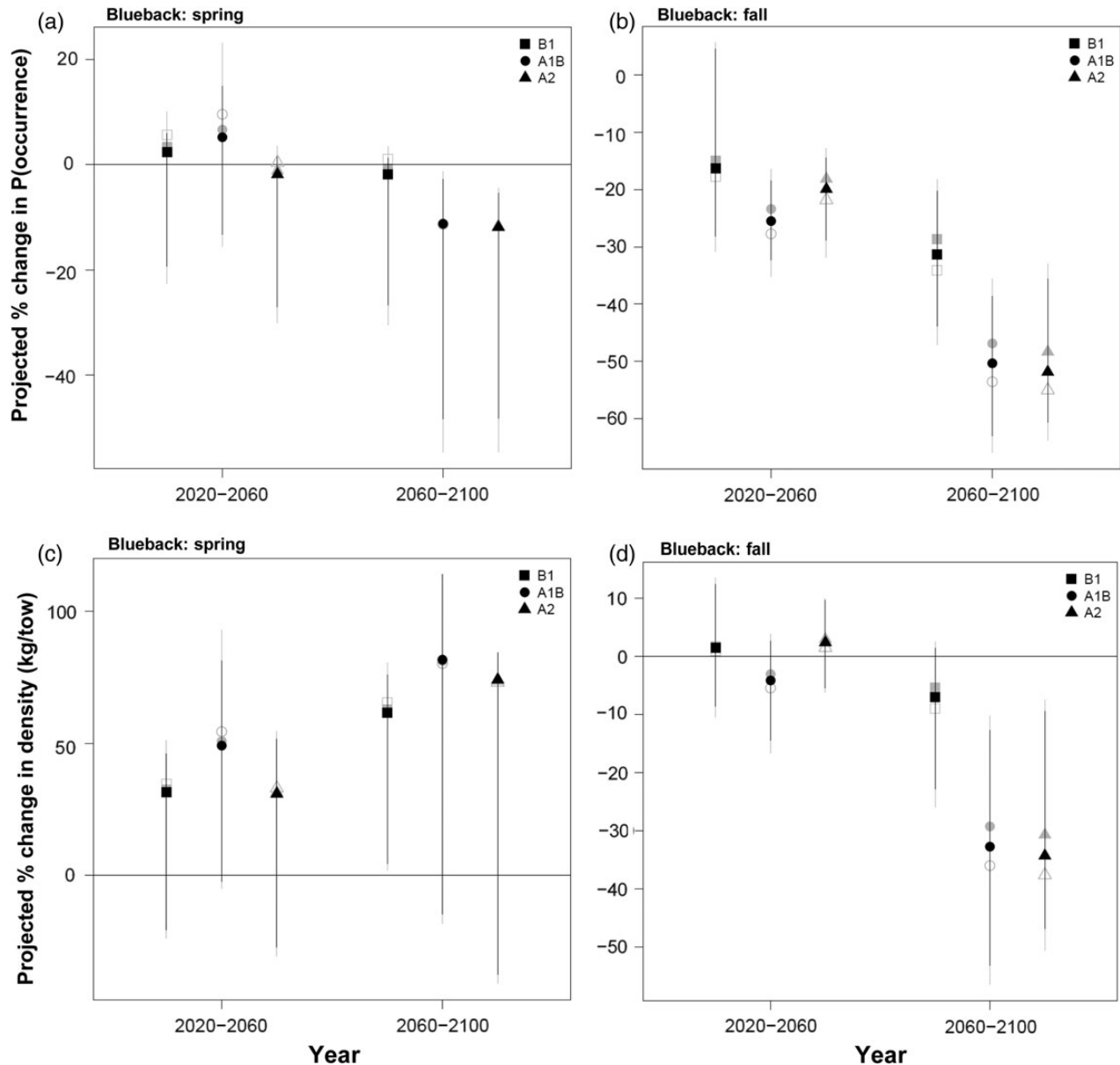
Overall, our projections isolate the potential effects of climate change, specifically ocean warming, and should not be interpreted as predictions of actual future abundances or distributions. True future population dynamics will be governed by many complex



**Figure 6.** Mean spatially aggregated per cent change in probability ( $P$ ) of occurrence (a and b) and density ( $\text{kg tow}^{-1}$ ; c and d) of alewife in spring (a and c) and fall (b and d) for two future periods in the Northwest Atlantic Ocean projected using an SDM linked with global climate projections. Projections were based on three emission scenarios (low—B1, moderate—A1B, and high—A2). Symbols correspond to ensemble mean temperature projections, where the range encompasses projections using eight individual climate models. Three alewife abundance scenarios, relative to historical abundance, were considered: low (gray empty), average (black filled), and high (gray filled).

human and ecosystem interactions that were not explicitly modelled in our study, and some of these processes, such as the distribution of dams throughout river herring spawning habitat, represent significant stressors (Hall *et al.*, 2011, 2012). In reality, climate change effects will not be disentangled from other factors, and in fact, effects due to other stressors may be magnified by climate change (Planque *et al.*, 2010; Shelton and Mangel, 2011). However, we focused exclusively on the effects of increasing ocean temperatures, in part because prudent natural resource management should account for the potential effects of climate change, but also because the confidence surrounding projections of future ocean temperatures is relatively high compared with projections of other stressors.

While not explicitly modelled, we did conduct a coarse assessment of the interactive effects of climate change and other stressors by evaluating the importance of initial population size in our projections of relative abundance. Substantial uncertainty surrounds historical population dynamics and stock statuses of alewife and blueback herring (ASMFC, 2012), so it is important to understand how populations of different sizes will respond to ocean warming. Sizes of spawning runs in many rivers have declined since 1999, but some runs have increased in recent years with concomitant increases in abundance in the trawl survey data we analysed (Figure 1; ASMFC, 2012). Regardless of initial population size, the direction of projected responses to climate change was similar for nearly all scenarios, but when population size was assumed to be



**Figure 7.** Mean spatially aggregated per cent change in probability ( $P$ ) of occurrence (a and b) and density ( $\text{kg tow}^{-1}$ ; c and d) of blueback herring in spring (a and c) and fall (b and d) for two future periods in the Northwest Atlantic Ocean projected using an SDM linked with global climate projections. Projections were based on three emission scenarios (low—B1, moderate—A1B, and high—A2). Symbols correspond to ensemble mean temperature projections, where the range encompasses projections using eight individual climate models. Three blueback herring abundance scenarios, relative to historical abundance, were considered: low (gray empty), average (black filled), and high (gray filled).

low, the magnitude of climate effects increased (i.e. increased sensitivity). Thus, effective conservation of river herring in the near term may increase their resiliency to future ocean warming. While this result hinges on the assumption that the historical effects of dynamic thermal habitat will be conserved, studies such as ours may help resource managers prepare for future climate change by informing conservation measures that increase resiliency in a changing ecosystem.

Using our SDM approach, we were able to project the likely distribution of river herring in terms of probability of occurrence as well as density. A common practice in habitat modelling is to use occupancy (i.e. presence/absence data) to characterize habitat,

especially if species are sampled with suboptimal gear (Hare *et al.*, 2012) or are rarely encountered (Gu and Swihart, 2004). However, maps based on presence/absence data may be overly optimistic. This binary approach presents occupied areas, but in areas where suitable habitat is marginal at best, biomass, density, and probability of detection may actually be low. Thus, we projected density and probability of occurrence to infer population-level dynamics rather than only characterize distributions. However, there are drawbacks and a number of assumptions underlying our SDM approach that should be considered. First, our models do not provide a mechanistic understanding of the relationship between climate change and river herring population dynamics. Rather,



our key assumption is that river herring distributions are governed by thermal regimes with temperature variables serving as simple proxies for complex physiological processes. This type of assertion is common to SDMs, and while this knowingly overlooks other factors that affect river herring distributions, there is strong evidence that many species exhibit preferred thermal ranges and distribute according to climate, at least at large scales (Araújo and Peterson, 2012). Another strong assumption of our models is that of equilibrium conditions across habitats and life stages in future periods. In other words, we assumed that the estimated thermal niches are conserved (i.e. no physiological evolution or adaptation), and as previously mentioned, that temperature is the only variable affecting future distributions (i.e. we isolated the climate effects). An implicit assumption of our models is that the trawl survey data we analysed were able to capture the true spatial and temporal patterns exhibited by river herring populations. While these data were likely the best available for conducting our analyses, it should be recognized that the bottom trawl survey was not originally designed to monitor pelagic species like river herring (Azarovitz, 1981; Sosebee and Cadrin, 2006). However, we analysed a subset of the data in an effort to reduce potential sampling biases.

Climate change represents an anthropogenic stressor that has the potential to significantly alter the distribution and abundance of anadromous fishes (Graham and Harrod, 2009; Petitgas *et al.*, 2012). In this study, we followed a general SDM approach to shed light on potential large-scale changes in river herring dynamics in the Northwest Atlantic Ocean. We demonstrated that, when integrated across stocks, river herring are vulnerable to the effects of ocean warming. However, we show that conservation efforts that promote high-population abundance in the near-term will likely benefit river herring populations over the long term by making them more resilient to the effects of climate change. A consequence of our focus on river herring in their marine phase is that considerable uncertainty remains regarding climate change effects on individual river runs. To strengthen the conclusions of our study, we recommend additional complementary work in select freshwater systems. Further, our analyses followed one of several potential methods for assessing climate effects on river herring and we encourage future studies that build upon our work and address associated uncertainties.

### Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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